RELEVANCE OF CRYPTIC FISHES IN BIODIVERSITY ASSESSMENTS: A CASE STUDY AT BUCK ISLAND REEF NATIONAL MONUMENT, ST. CROIX

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ABSTRACT

Because cryptic fishes are difficult to accurately survey, they are undersampled components of coral reef habitats, and their ecological roles have been generally ignored. Fifty-eight enclosed stations were sampled in shoreline, nearshore reef, lagoon, backreef, forereef, and bank/shelf habitats with an ichthyocide (rotenone) at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Our samples included 55 families and 228 species, 60 previously unreported from St. Croix. Fish assemblages varied across habitat zones with the shoreline assemblage the most distinct. Only 8% of the species were present in all habitats. Multi-dimensional scaling plots of habitat characteristics and Bray-Curtis similarities of fish assemblages revealed similar patterns. Dominant and rare taxa are enumerated for each habitat sampled. Rotenone and visual census data are compared. While visual surveys accumulated more species per unit of effort, rotenone samples accumulated more species by area. Only 36% of the 228 species sampled with rotenone were visually detected, while 70% of the 115 species visually detected were also collected with rotenone. The use of rotenone is controversial but important for obtaining reasonably complete inventories of reef fishes. Misconceptions about rotenone and the advantages and limitations of alternative biodiversity assessment methods are discussed.

Managers of marine protected areas (MPAs) generally recognize the importance of fish biodiversity in reef ecosystems, yet a reasonably complete picture of that biodiversity is frequently lacking. Coral reef ecosystems are so structurally and biologically complex, and reef-fish life histories and behavior so diverse, no single assessment technique can provide resource managers and scientists with unbiased qualitative or quantitative estimates of reef-fish assemblages (Sale and Douglas, 1981; Bortone et al., 1986; Ackerman and Bellwood, 2000). Nevertheless, a reasonably complete baseline inventory is desirable for estimating biodiversity, comparing the composition of ichthyofaunas at different locations, and evaluating the success of future management actions and the impacts of threats (e.g., overfishing, pollution). Census techniques routinely used to detect highly mobile or easily observable species will likely miss or significantly underestimate morphologically or behaviorally cryptic species that are usually hidden among intricate substrata. Both readily observable and cryptic fishes have complex ecological and behavioral interrelationships, and human and natural events that alter coral reefs impact the entire fish community. By supplementing data obtained from studies of visible fauna with collections of cryptic organisms, a more complete assessment can be achieved. The use of ichthyocides to investigate coral reef fish communities is controversial because some reef biologists consider it to be an unnecessarily consumptive sampling method. The objectives of this paper are to: (1) present a base-line inventory of cryptic reef and shoreline fishes inhabiting shallow-water habitats at Buck Island Reef National Monument; (2) compare fish distributions and relative abundance patterns among the sampled habitats; (3) compare the results of ichthyocide (rotenone) sampling with independently

conducted underwater visual censuses (UVC); and (4) discuss misconceptions about rotenone and suggest guidelines for its use in marine habitats.

Materials and Methods

STUDY SITES.—Buck Island Reef National Monument (BIRNM), one of the first MPAs in the Caribbean, is located off the northeast end of St. Croix, the largest of the U.S. Virgin Islands (Fig. 1). St. Croix is geologically separated from the rest of the Virgin Islands by the 4685 m-deep and 60 km-wide Virgin Islands trough. Prevailing winds are from the northeast or southeast, depending on season. When established in 1961, the monument consisted of 283 ha of water surrounding the 72 ha island. Buck Island lacks freshwater drainage, estuarine or mangrove habitats, and tidal fluctuation is minimal. The "marine garden" (188 ha), including the entire south lagoon and most of the north lagoon from shoreline to beyond the encircling linear reef, was technically a "no-take" zone, but some fishing continued within and adjacent to the area and BIRNM did not function as a strict marine reserve (Rogers and Beets, 2001). Elsewhere within the monument, taking of fishes with recreational gear and traps of conventional Virgin Islands design was allowed, although some illegal trap fishing continued. The monument was enlarged by 7339 ha, an area extending roughly from the original northern boundary to the edge of the shelf, by Presidential Proclamation on January 17, 2001. After much public discussion and congressional hearings, all extractive fishing activities within and immediately adjacent to the BIRNM original boundaries are now prohibited in accord with compelling evidence indicating that greater protection was necessary to prevent the continued decline of fishery resources in the U.S. Virgin Islands (Rogers and Beets, 2001). Natural stresses caused by recent major hurricanes have also affected the reef ecosystem of BIRNM, including Hurricanes David in 1979 (Rogers et al., 1982) and Hugo in 1989 (Bythell et al., 1993). Hurricane Hugo, which passed directly over the island, resulted in a significant decrease in coral cover at some forereef sites. A combination of white band disease and storm damage also contributed to a decrease in elkhorn coral, Acropora palmata, cover from 85% (1976) to 0.8% (1989) with very limited recruitment as of 2001. Most of St. Croix, including Buck Island, suffered a mass die-off of the grazing sea urchin Diadema antillarum in 1983-84 with a corresponding increase in macroalgal cover. After 17 yrs of negligible recovery, the urchin population appears to be rebounding (Miller et al., 2003). Because the primary objective of this study was to inventory the nearshore reef fishes as part of the National Park Service National Vascular Plant and Vertebrate Inventory Program, multiple habitats were sampled (Fig. 1). Station locations were predetermined by stratified random selection based on National Oceanographic and Atmospheric Administration (NOAA) habitat layers in a geographical information system (GIS, see below). Some sites were eliminated because the topography of the reef and shallow depth prevented the research vessel from getting sufficiently close to the area or the substrate was unsuitable for erection of an enclosure blocknet. Distances between adjacent stations, combined with the direction and intensity of prevailing currents, were sufficient to ensure that collecting activities did not affect species compositions and abundances at other sites. Stations were renumbered for ease of text discussion and do not indicate the sequence in which the sites were sampled. Sampling stations were classified into six habitat zones (Table 1).

Shoreline (sta. 1–15).—Sampling was conducted as close to shore as possible, primarily in the intertidal zone, about 1–5 m from shore with the distance dictated by water depth and bottom slope. The southwest shore of Buck Island is mostly bare sandy beach and for that reason was not sampled. Stations 4–10 are more exposed to strong battering waves than the other shoreline stations.

Nearshore Reef (sta. 16–17).—These two relatively shallow stations had little relief and were 34 and 62 m, respectively, from shore. Although clearly not patch reefs, both stations were so intermediate in topography and composition that we were unable to objectively assign them to one of the other categories and therefore treated them as a separate habitat zone.

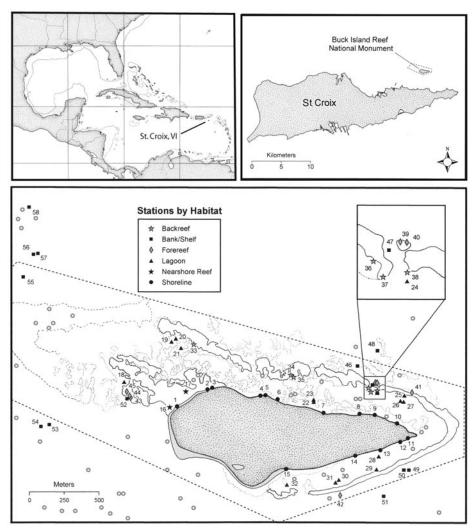


Figure 1. Maps of Caribbean Sea, St. Croix, USVI, and Buck Island Reef National Monument (BIRNM) showing locations of 58 rotenone collection stations and the historical monument boundary. Open circles indicate locations of NOAA visual transect and point counts. Exposed and submerged reef crests are outlined.

Patch Reefs in Lagoon (sta. 18–32).—These reefs are completely isolated from other coral reef formations by sand, seagrass, or other habitats and have no structural axis relative to contours of the shore or shelf edge. Patch reefs may consist of single dome-shaped structures or clusters of small aggregate reefs. Patch reefs in lagoons are defined as those that are partially or completely buffered from high-energy waves by a linear reef, including ones that do not break the surface.

Backreef (sta. 33–38).—Habitat that is continuous with, and typically on, the landward side of a linear reef and protected from high-energy waves by the reef crest is identified as backreef.

Forereef (sta. 39–45).—This reef habitat is on or immediately adjacent to the seaward edge of a linear reef crest. Stations 39–40 were made on the seaward side of a massive pinnacle-like reef or "haystack." These steep-sided patch reefs are comprised primarily of broken, en-

Table 1. Station numbers, geographical coordinates, habitat zones and descriptors, distance to shore, depth measurements, percent areal coverage of seagrass, sand, cobble, boulder, bedrock, dead coral, live coral, presence of soft coral, stature of algae, and extent of algae for 58 rotenone samples made in July-August 2001 at BIRNM.

Station	Original	North	West	Zone	Habitat descriptor	Distance to shore	Distance to shore Minimum depth Maximum depth	Maximum depth	Relief
numper	numper	latitude	longitude			(m)	(m)	(m)	(m)
1	12	17.47	64.37	Shoreline	Colonized bedrock	_	0.1	0.7	0.3
2	6	17.47	64.37	Shoreline	Colonized bedrock	4	0.2	0.4	0.2
3	∞	17.47	64.37	Shoreline	Colonized bedrock	1	0.3	0.5	0.3
4	1	17.47	64.37	Shoreline	Colonized bedrock	1	0.2	0.5	0.3
5	2	17.47	64.37	Shoreline	Colonized bedrock	2	0.1	8.0	0.5
9	9	17.47	64.37	Shoreline	Colonized bedrock	5	0.2	8.0	0.5
7	3	17.47	64.37	Shoreline	Colonized bedrock	1	0.0	8.0	0.7
8	99	17.47	64.37	Shoreline	Colonized bedrock	1	0.4	0.4	0.2
6	7	17.47	64.37	Shoreline	Colonized bedrock	1	0.1	0.5	0.4
10	10	17.47	64.36	Shoreline	Colonized bedrock	1	0.4	1.0	9.0
11	5	17.47	64.36	Shoreline	Colonized bedrock	1	0.0	0.5	0.3
12	4	17.47	64.36	Shoreline	Colonized bedrock	1	0.0	9.0	0.2
13	15	17.47	64.36	Shoreline	Seagrass/Colonized bedrock	1	0.1	0.4	0.3
14	11	17.47	64.37	Shoreline	Colonized bedrock	1	0.3	0.7	0.5
15	17	17.47	64.37	Shoreline	Colonized bedrock/Sand	1	0.3	8.0	0.2
16	14	17.47	64.37	Nearshore reef	Nearshore reef Colonized bedrock	34	6.0	1.1	0.2
17	13	17.47	64.37	Nearshore reef Linear reef	Linear reef	62	0.3	1.1	0.5
18	35	17.47	64.38	Lagoon	Patch reef/Sand	402	3.0	5.0	2.0
19	26	17.47	64.37	Lagoon	Patch reef /Pavement	412	1.0	3.0	2.0
20	25	17.47	64.37	Lagoon	Patch reef /Pavement	419	2.7	4.4	1.7

Table 1. Continued.

ercent seagrass	Percent sand	Percent cobble	Percent boulder	Percent bedrock	Station Percent seagrass Percent sand Percent cobble Percent boulder Percent bedrock Percent dead coral Percent live coral number	Percent live coral	Soft coral	Algae stature	Algae extent
	25	15	50	10	ı	I	ı	1	1
	25	10	30	35	I	I	I	7	2
	I	10	50	40	I	I	I	7	3
	5	5	80	10	I	ĺ	I	-	3
1	5	5	80	10	I	ĺ	I	-	3
	S	5	40	45	I	5	I	3	2
I	30	10	40	20	I	I	I	-	2
ı	ĺ	ĺ	5	06	I	5	I	7	3
1	5	10	15	70	I	I	I	3	3
I	I	15	30	50	I	5	I	3	2
	5	15	30	50	I	I	I	3	3
15	5	10	45	20	I	5	I	7	3
	5	5	15	50	I	I	I	1	_
	5	15	20	30	20	5	I	2	2
ı	25	25	25	25	I	ĺ	I	-	_
ı	5	10	65	20	I	I	I	3	1
ı	5	5	15	50	15	10	I	1	2
I	15	I	5	I	40	40	1	-	_
	5	5	I	30	45	15	1	-	2
	10	5	I	10	45	30	1	-	2

Table 1. Continued.

Station Original	North	West	Zone	Habitat descriptor	Distance to shore	Minimum depth	Maximum depth	Relief
24	`	64.37	Lagoon	Patch reef/Sand	343	3.4	4.5	1.1
50		64.37	Lagoon	Colonized bedrock	52	1.0	3.5	2.5
51	17.47	64.37	Lagoon	Patch reef/Sand	29	2.7	4.2	1.5
33	17.47	64.36	Lagoon	Patch reef /Pavement	163	3.8	4.3	0.5
31	17.47	64.36	Lagoon	Linear reef	210	1.0	3.3	2.3
20	17.47	64.36	Lagoon	Patch reef/Sand	165	2.4	4.4	2.0
21	17.47	64.36	Lagoon	Patch reef/Sand	165	3.7	4.6	6.0
16	17.47	64.36	Lagoon	Patch reef/Sand	50	1.3	1.6	6.0
48	17.47	64.36	Lagoon	Patch reef/Sand	137	0.3	1.3	1.0
40	17.47	64.37	Lagoon	Patch reef /Sand	133	1.3	2.3	1.0
38	17.47	64.37	Lagoon	Patch reef/Sand	144	1.5	2.5	1.0
28	17.47	64.37	Lagoon	Patch reef /Sand	113	2.0	3.5	1.5
46	17.47	64.37	Backreef	Patch reef /Sand	342	2.6	3.6	1.0
55	17.47	64.37	Backreef	Linear reef	214	3.0	4.4	1.4
54	17.47	64.37	Backreef	Linear reef	210	2.3	5.3	3.0
19	17.47	64.37	Backreef	Patch reef/Minimal sand	194	1.5	2.8	1.3
34	17.47	64.37	Backreef	Linear reef	166	1.8	4.8	3.0
18	17.47	64.36	Backreef	Patch reef/Sand	180	3.0	4.5	1.5
27	17.47	64.37	Forereef	Haystack reef	228	9.3	12.3	3.0
32	17.47	64.37	Forereef	Haystack reef	228	8.0	11.0	3.0

Table 1. Continued.

Algae	2	7	7	1	2	7	1	1	2	1	1	3	7	7	2	1	1	1	7	2
Algae	_	-	_	_	_	2	_	_	_	-	_	3	2	_	_	_	_	_	_	_
Soft	_	-	_	_	_	_	_	_	1	-	_		-	П	_	_	_	П	_	_
Percent live coral	50	5	10	10	15	5	20	30	25	30	25	I	10	5	10	30	15	15	S	1
sand Percent cobble Percent boulder Percent bedrock Percent dead coral Percent live coral Soft coral	30	75	75	35	55	06	40	35	55	50	45	85	75	70	65	20	75	35	85	06
Percent bedrock	I	I	I	30	20	I	10	I	I	ı	5	I	ı	I	I	25	I	20	I	I
Percent boulder	1	I	1	S	1	1	1	1	I	1	1	1	1	I	1	1	1	I	1	1
Percent cobble	5	I	I	I	I	I	I	5	I	1	I	I	1	I	I	5	I	I	I	I
Percent sand	15	20	15	20	10	5	30	30	20	20	25	15	15	25	25	20	10	30	10	10
Station Percent seagrass Percent number	I	I	I	I	I	I				1	I		1	I	I	I	I		I	I
Station	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40

Table 1. Continued.

criptor Distanc	Habitat descriptor	West Zone Habitat descriptor longitude	longitude
	Forereef Linear reef 249	64.36 Forereef Linear reef	64.36 Forereef Linear reef
	Forereef Linear reef 24	64.37 Forereef Linear reef	64.37 Forereef Linear reef
	Forereef Linear reef 30	64.38 Forereef Linear reef	64.38 Forereef Linear reef
atch reef/Sand 314	Forereef Patch reef/Sand 31	64.38 Forereef Patch reef/Sand	64.38 Forereef Patch reef/Sand
	Forereef Patch reef /Pavement 34	64.38 Forereef Patch reef /Pavement	Forereef Patch reef /Pavement
atch reef/Sand 351	Bank/Shelf Patch reef/Sand 35	64.37 Bank/Shelf Patch reef/Sand	64.37 Bank/Shelf Patch reef/Sand
atch reef/Sand 226	Bank/Shelf Patch reef/Sand 2	64.37 Bank/Shelf Patch reef/Sand	64.37 Bank/Shelf Patch reef/Sand
aystack reef	Bank/Shelf Haystack reef	64.36 Bank/Shelf	64.36 Bank/Shelf
atch reef/Sand	Bank/Shelf Patch reef/Sand	64.36 Bank/Shelf	64.36 Bank/Shelf
atch reef/Sand	Bank/Shelf Patch reef/Sand	64.36 Bank/Shelf	64.36 Bank/Shelf
atch reef /Sand	Bank/Shelf Patch reef /Sand	64.36 Bank/Shelf	64.36 Bank/Shelf
atch reef/Sand	Bank/Shelf Patch reef/Sand	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef/Sand	Bank/Shelf Patch reef/Sand	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef/Sand	Bank/Shelf Patch reef/Sand	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef /Sand channels	Bank/Shelf Patch reef /Sand channels	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef /Sand channels	Bank/Shelf Patch reef /Sand channels	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef /Sand channels	Bank/Shelf Patch reef /Sand channels	64.38 Bank/Shelf	64.38 Bank/Shelf
atch reef /Sand channels	Bank/Shelf Patch reef /Sand channels	64.38 Bank/Shelf	64.38 Bank/Shelf

Table 1. Continued.

Station	Station Percent seagrass Percent	Percent sand	Percent cobble	Percent boulder	Percent bedrock	sand Percent cobble Percent boulder Percent bedrock Percent dead coral Percent live coral	Percent live coral	Soft	Algae	Algae
number								coral	stature	extent
41	I	10	I	I	1	09	30	-	1	2
42	I	20	I	I	5	30	45	_	_	_
43	I	15	I	5	15	09	5	_	2	3
4	I	15	5	I	10	65	5	_	2	2
45	I	5	I	I	I	75	20	_	2	2
46	I	20	I	I	5	70	5	_	_	2
47	I	15	I	I	I	45	40	1	1	2
48	I	15	I	I	1	75	10	П	1	-
49	I	25	I	I	1	20	55	_	1	-
50	I	10	I	I	10	20	09	_	_	_
51	I	30	I	I	10	50	10	1	2	1
52	I	15	5	I	I	50	30	_	2	2
53	I	30	I	I	1	65	5	_	_	_
54	I	25	I	I	I	70	5	1	1	1
55	I	15	I	I	1	75	10	П	1	2
99	I	20	I	5	5	65	5	-	1	_
57	I	20	I	I	10	09	10	_	_	_
58	I	20	I	I	I	75	5	-	-	1

crusted, and cemented fragments of *A. palmata*, and their geological relationship to the main barrier reef is unclear (Hubbard, 1991).

Reefs on Bank Shelf (sta. 46–58).—This category is probably the most heterogeneous with respect to habitat. Bank shelf is defined as the flattened platform seaward of the forereef or between the shoreline and the open ocean if no protective linear reef is present. Included are isolated patch reefs in relatively deep water (8–15 m) including one haystack (see above). A few stations were closely adjacent to linear forereefs, while others (sta. 55–58) were far offshore and aligned in a series of rows separated by sandy channels.

Habitat Characterization.—Benthic habitat maps produced by NOAA's Center for Coastal Monitoring and Assessment Biogeography Program (Kendall et al., 2001) were used to identify and locate broadly defined habitats. NOAA-defined habitat zones included in the samples were: shoreline intertidal, lagoon, backreef, reef crest, forereef, and bank/shelf. A handheld global positioning system (GPS) and a field base map were used to locate sites. Prior to sampling, an underwater video recording was made at each station to characterize the habitat, and measurements of depth and relief were also taken. Videos were analyzed and percent areal coverage of seagrass (*Thalassia*), sand, cobble, boulder, bedrock, dead coral, and live coral were estimated. Live corals were mostly *Diploria* and *Montastraea*, but *Acropora*, *Agaricia*, *Dendrogyra*, and *Porites* were also present. The presence of gorgonians was also recorded. Algae stature was evaluated as (1) encrusting; (2) medium, up to 10-cm height; or (3) tall, > 10 cm. Algal extent was either (1) sparse, 20% or less areal coverage; (2) moderate, 21%–80%; or (3) complete, > 80%. Distance to shore was based on GIS measurements.

FISH SAMPLING METHODOLOGY.—The natural insecticide rotenone, which is found primarily in South American plant genus *Derris*, has traditionally been used for scientific purposes as an ichthyocide to collect small, shallow-water reef fishes (Smith, 1973). We used dried 8% rotenone powder, which is commonly available in 5% strength. Each sample station was surrounded with 3-mm mesh blocknet weighted with a solid core leadline sufficient to provide a tight seal with the bottom and enough floats to make the 1.2-m high net stand fully erect in slight to moderate current. At shallow shoreline sites vertical lengths of PVC pipe, attached at regular intervals along the length of the net, were used to help keep it erect, and the leadline was reinforced with large boulders to counteract the force of waves and strong surge. Size of stations enclosed by the blocknet ranged from 7.6 to 18 m². At sites where scuba was used, the outer periphery of the net was positioned about 1 m from the reef for the pair of divers to have room to swim and pick up specimens on the adjacent substrate.

Approximately 0.5-1 kg of rotenone powder was mixed in a bucket of seawater and a generous amount of nontoxic, biodegradable liquid detergent, which acts as a safe and effective surfactant, was added to make a thick slurry. The mixture was then sealed in sturdy plastic bags equipped with a push nozzle and cap. The rotenone was dispersed as completely as possible at each site, including under ledges and in tiny crevices. Small handnets were used to collect affected fishes. Because fishes have different levels of rotenone tolerance, with sanddwelling eels usually the last to be affected, two divers made continuous searches inside the net enclosure for 30-45 min before attempting to collect fishes killed outside the net area. Gobies, small blennioid fishes, and juveniles are some of the first to succumb to rotenone and become dislodged from their hiding places, therefore an initial concentrated effort was made to collect these fish before they are taken by predators. With the exception of a relatively few schooling species, such as damselfishes of the genus Chromis, most cryptic reef fishes maintain close enough contact with the substrata that the net height prevented them from drifting out of the enclosure (although strong waves at some of the shoreline stations were a major problem). An effort was made to recover as many specimens as possible, both within and outside the blocknet. Primary effort was devoted to fishes inside the net enclosure where the density of fish per unit area could be reliably determined. Collections made inside or outside the blocknet were analyzed separately.

UNDERWATER VISUAL CENSUS (UVC) METHODS.—The number of species obtained using rotenone at 58 stations during July–August, 2001 was compared with the number of spe-

cies observed by NOAA divers during August–September, 2001 using both belt transect (Christensen et al., 2003) and point-count (Bohnsack and Bannerot, 1986) methods at each of 70 stations adjacent to Buck Island (45 of these UVC sites are shown in Figure 1). Detailed descriptions of these visual census methods are available at http://www.ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish/protocols.html. Transects were 25-m long and 4-m wide and required 15 min to complete; point counts included all species in a 7.5-m radius with 5 min allowed for identifications.

IDENTIFICATION SOURCES, AUTHORITIES, AND VOUCHER SPECIMENS.—Species identifications were based primarily on Carpenter (2003), the many relevant references cited in that work and comparisons with other voucher specimens. Correct identification of a few taxa was dependent on recent taxonomic studies (Tyler and Tyler, 1997; Williams and Mounts, 2003; Williams and Tyler, 2003; Møller et al., 2004, 2005). When applicable, common and scientific names of fishes are those used by Smith (1997), Carpenter (2003), and Nelson et al. (2004); in a few cases we could not find an available common name and created one. Authorities and year of publication of all listed fish species are available in the periodically updated on-line edition of Eschmeyer (1998).

Many small cryptic marine fishes cannot be reliably identified in the field and must be examined under a microscope usually in conjunction with detailed taxonomic literature references. Specimens obtained during this study are deposited in the Florida Museum of Natural History (FLMNH). The periodically updated database for this material and associated collection data are available at http://www.flmnh.ufl.edu/fish/collection/collectdata.htm.

STATISTICAL ANALYSIS.—Multi-dimensional scaling (MDS) using PRIMER 5 software (Clarke and Warwick, 2001) was applied to habitat and fish density data. Because of the varied nature of the habitat data (Table 1), normalized Euclidean distance matrices were used in habitat MDS. Fish species densities (number m⁻²) were square-root transformed to balance common and rare species. Bray-Curtis similarity matrices of transformed fish densities between samples were used to compile fish community MDS. All MDS procedures used 50 iterations and were checked for convergence. Stress values are measures of the distortion between the distance of the ranking of the MDS configuration and the analogous rankings in the dissimilarity matrix. Smaller stress values indicate greater confidence in the pattern. Plots with stress values exceeding 0.2 are generally unreliable. Species accumulation curves were developed using Estimates software (Colwell, 2001; Colwell et al., 2004).

RESULTS

The number and diversity of species were not uniformly distributed across habitats (Fig. 2), with only 8% of 228 sampled species present in all habitats. The multi-dimensional scaling plot of habitat variables (see Table 1) revealed marked differences between sites along the shore (shoreline, nearshore reef) and the other zones (Fig. 3A). The stress value of this two-dimensional pattern is < 0.2 and hence considered to be a reliable representation (Clarke and Warwick, 2001). Station 13 was an outlier primarily because 25% of its area consisted of the seagrass *Thalassia testudinum* (Table 1). Bank/shelf patch reefs clustered somewhat separately from the forereef, backreef, and lagoon sites. Distance from shore and depth parameters contributed to this pattern. Station 52, however, plotted in the midst of those three zones. Forereef, backreef, and lagoon sites averaged more than 50% cover in dead coral and were not distinguishable in the habitat MDS, even when shoreline and nearshore reef data were excluded.

MDS plots of fish densities showed that fish community structure generally followed our pre-assigned habitat zones based on NOAA classifications and benthic habitat maps of the area. Most shoreline stations were tightly grouped and separate

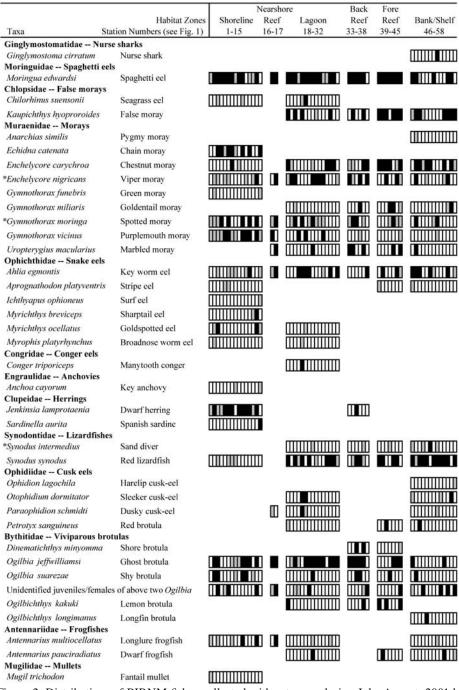


Figure 2. Distributions of BIRNM fishes collected with rotenone during July–August, 2001 by habitat zones and collection stations; black bars = present inside station; grey bars = present adjacent to station; white bars = absent from station; blank = absent from zone. Asterisks indicate species that were also observed in 70 NOAA visual surveys during August–September, 2001.

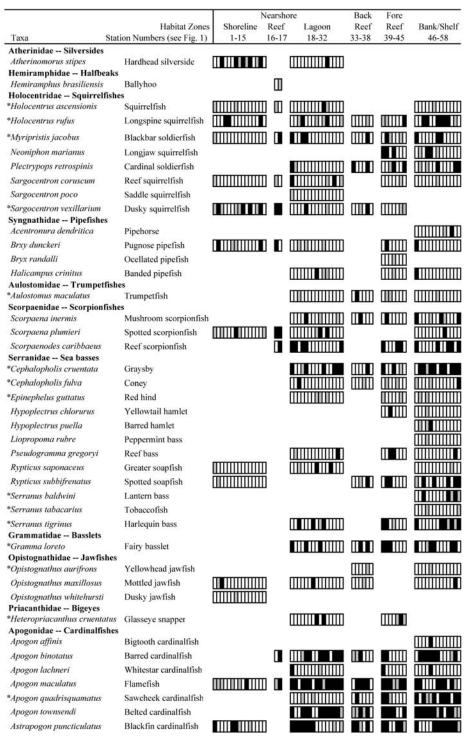


Figure 2. Continued.



Figure 2. Continued.

	contact of	N	earsho	re	Back	Fore	
Taxa	Habitat Zones Station Numbers (see Fig. 1)		Reef 16-17	Lagoon 18-32	Reef 33-38	Reef 39-45	Bank/Shelf 46-58
Xyrichtys novacula	Pearly razorfish		10 17	 	55.50	07 10	
*Xyrichtys splendens	Green razorfish						
Scaridae Parrotfishes							
*Cryptotomus roseus	Bluelip parrotfish						
*Scarus iseri	Striped parrotfish				Ш		
*Scarus taeniopterus	Queen parrotfish						
*Scarus vetula	Princess parrotfish						***************************************
*Sparisoma atomarium	Greenblotch parrotfish						
*Sparisoma aurofrenatum	Redband parrotfish						
*Sparisoma chrysopterum	Redtail parrotfish						
*Sparisoma radians	Bucktooth parrotfish						
*Sparisoma rubripinne	Redfin parrotfish						
*Sparisoma viride	Stoplight parrotfish					11 11	
Trypterygiidae - Triplefi Enneanectes altivelis							
Enneanectes boehlkei	Lofty triplefin		п		-		
Enneanectes pectoralis	Roughhead triplefin		H				
Dactyloscopidae Sand s	Redeye triplefin targazers	шшшшшш	Ш		Ш	шшш	
Dactyloscopus poeyi	Shortchin stargazer						
Dactyloscopus tridigitatus	Sand stargazer						
Gillellus greyae	Arrow stargazer						
Gillellus uranidae	Warteye stargazer						
Platygillellus rubrocinctus	Saddle stargazer		-			III	
Labrisomidae Scaly ble							
Labrisomus albigenys	Whitecheek blenny		_		ШШ	ЩЩ	
Labrisomus bucciferus	Puffcheek blenny					ШШ	
Labrisomus gobio	Palehead blenny		_		Ш		
Labrisomus guppyi	Mimic blenny					Ш	
Labrisomus haitiensis	Longfin blenny	190 to 100 to	_			111	
Labrisomus nigricinctus	Spotcheek blenny						
Labrisomus nuchipinnis	Hairy blenny		_				
Malacoctenus aurolineatus	Goldline blenny						
*Malacoctenus boehlkei	Diamond goby	W			-		
Malacoctenus erdmani	Imitator blenny						
Malacoctemus gilli	Dusky blenny						
Malacoctenus macropus	Rosy blenny						
*Malacoctenus triangulatus	Saddle blenny						
Malacoctenus versicolor	Barfin blenny						
Paraclinus fasciatus	Banded blenny						
Paraclinus grandicornis	Horned blenny						
Paraclinus nigripinnis	Blackfin blenny						
Starksia atlantica	Smootheye blenny						
Starksia culebrae	Culebra blenny						
Starksia elongata	Elongate blenny						
Starksia lepicoelia	Blackcheek blenny						
Starksia melasma	Blackspot blenny			12	A 18		
Starksia nanodes	Dwarf blenny						
Starksia smithvanizi	Brokenbar blenny						
			-				

Figure 2. Continued.

	Habitat Zones	Shoreline	learsho Reef	Dre Lagoon	Back Reef	Fore Reef	Bank/Shelf
Taxa Stati	ion Numbers (see Fig. 1)	1-15	16-17	18-32	33-38	39-45	46-58
Chaenopsidae Tube blennie	es						
Acanthemblemaria aspera	Roughhead blenny				Ш		
Acanthemblemaria spinosa	Spinyhead blenny						
*Chaenopsis limbaughi	Yellowface blenny						
Emblemaria pandionis	Sailfin blenny						
Emblemariopsis bahamensis	Blackhead blenny						
Emblemariopsis ruetzleri	Carrie Bow blenny						
Emblemariopsis signifer	Flagfin blenny			V. 2007 (2007 12 - 12 00 00 00 00 00 00 00 00 00 00 00 00 00			
Emblemariopsis sp.	blenny						
Stathmonotus gymnodermis	Naked blenny						
Stathmonotus stahli tekla	Eelgrass blenny						
Blenniidae Combtooth blen					mm		
Entomacrodus nigricans	Pearl blenny	II III					
Hypleurochilus springeri	Orangespotted blenny		1				
Hypsoblennius exstochilus	Longhorn blenny				men		
*Ophioblennius macclurei	Redlip blenny						ШШШШШ
Scartella cristata Gobiesocidae Clingfishes	Molly miller		J				
Acyrtus artius	Papillate clingfish	пт	i	ппппппппппппппппппппппппппппппппппппппп		ПППП	
Acyrtus rubiginosus	Red clingfish		П			•	
Gobiesox nigripinnis	Blackfin clingfish						
Gobiesox punctulatus	Stippled clingfish	1 11 1 1111	í				
Tomicodon reitzae	Surge clingfish		i				
Callionymidae Dragonets	ouige emignon		1				
*Paradiplogrammus bairdi	Lancer dragonet						
Gobiidae Gobies	D. J. 126						
Barbulifer antennatus	Barbulifer		1				
Bathygobius soporator	Island frillfin		J			-	
*Coryphopterus dicrus	Colon goby				Ш		
*Coryphopterus glaucofraenum	Bridled goby						
Coryphopterus personatus	Masked goby				Щ		1 111 11
Coryphopterus thryx	Bartail goby				ШШ	ЩЩ	IIIIII I
*Ctenogobius saepepallens	Dash goby					ШШШ	
Elacatinus chancei	Shortstripe goby						
Elacatinus dilepis	Orangeside goby					ШШ	
*Elacatinus evelynae	Sharknose goby		-		Ш		
Elacatinus gemmatum	Frecklefin goby				Ш		шшшшш
Elacatinus pallens	Semiscaled goby					Ш	
Elacatinus prochilos	Broadstripe goby				Ш		
Ginsburgellus novemlineatus	Ninelined goby		J _				
*Gnatholepis thompsoni	Goldspot goby			<u> </u>			
Lythrypnus crocodilus	Mahogany Goby				Ш		
Lythrypnus elasson	Dwarf goby						
Lythrypnus nesiotes	Island goby						
Lythrypnus okapia	Okapi goby				-		
Priolepis hipoliti	Rusty goby						
Psilotris alepis	Scaleless goby						
Psilotris boehlkei	Popeye goby						
Psilotris celsus	Highspine goby		3 15100		·		
Pycnomma roosevelti	President goby				Ш		

Figure 2. Continued.

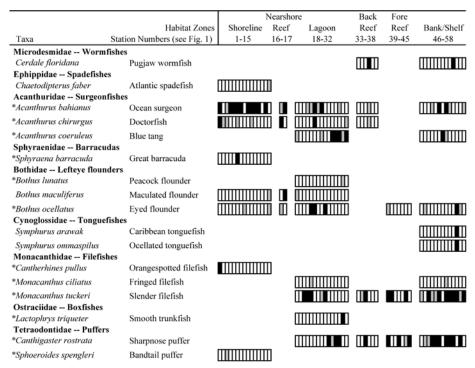


Figure 2. Continued.

from the other zones (Fig. 3B). Station 8 was problematic due to heavy surge that caused most fish to drift outside the enclosure. Stations 1 and 15, located in or adjacent to predominately bare sand habitat, also plotted separately from the other shoreline stations and included a preponderance of species that have an affinity for sand (e.g., Dactyloscopus tridigitatus) or an aversion to lack of cover (e.g., Ogilbia spp. and many blennies). Nearshore reef fishes plotted midway between the shoreline and the other zones, probably reflecting the intermediacy of the habitat. Because of the lack of separation in the offshore zones, a separate MDS of fish densities was plotted (Fig. 3C). While the stress value of 0.19 precludes reliance on precise sample positions in the plot, the pattern still merits discussion. The deeper and more offshore sites tended to cluster in the lower left and shallower inshore sites in the upper right. Bank/shelf sites clustered in the lower left corner of the plot except stations 47 and 52. Station 47 is located in a channel between a gap in the linear reef (Fig. 1), where the fish assemblage is probably strongly influenced by its hydrological and geographical proximity to the backreef (station 37) and lagoon stations (Fig. 3C). Although station 52 is a patch reef on the bank/shelf outside the linear reef, the fish assemblage was more similar to forereef (43-45) and lagoon (18) sites in the immediate area. Fish assemblages at several proximal sample sites were similar (Figs. 1, 3C) despite assignment to different habitat zone classifications. This is not surprising because the habitat and zone descriptors we used are based on generally accepted definitions (Kendall et al., 2001) that mostly apply to large scale features of marine environments and are incapable of adequately accounting for the ecological continuum and complex physical mosaic that is typical of reef ecosystems.

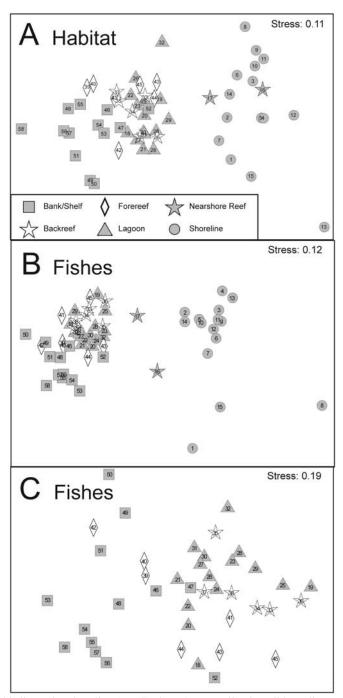


Figure 3. Multi-dimensional scaling (MDS) plots. A) normalized Euclidean distances between 58 stations based on the habitat parameters presented in Table 1; B) Bray-Curtis similarity distances between samples based on square-root transformed densities (number m⁻²) of 196 fish species collected inside blocknets at 58 rotenone stations; and C) Bray-Curtis similarity distances of 174 fish species from 41 rotenone stations (shoreline and nearshore reef excluded). Stress value indicates degree of confidence in the diagram.

Parameter			Habitat z	ones		
	Shoreline	Nearshore	Lagoon	Backreef	Forereef	Bank/ shelf
Number of stations	15	2	15	6	7	13
Mean fish density (# m ⁻²)	11.3	8.6	13.2	15.9	12.5	17.0
Standard deviation	12.2	7.8	7.1	7.3	5.8	8.8
Mean number of species	20.4	30.5	38.1	35.5	39.6	38.6
Standard deviation	9.6	19.1	9.6	6.2	5.8	7.0
Species unique to zone	18	0	5	0	3	17
(inside and outside of blocknet)						

Table 2. Mean fish densities, mean numbers of species, and numbers of unique species collected within six habitat zones at BIRNM in July–August, 2001.

Samples obtained from blocknet enclosures on bank/shelf reef sites had the highest mean densities of fish (Table 2). Shoreline stations had the highest variation in fish densities mostly due to the large number and patchy distribution of a schooling clupeid that accounted for 48% of the total density. Species diversity was higher for lagoon, backreef, forereef, and bank/shelf reef stations. Shoreline and bank/shelf reef habitats had the most species captured exclusively within those habitat zones.

The numerically dominant taxa in each habitat and those unique to a particular habitat are discussed below. Summary information refers to statistics for fishes collected only inside the blocknet (Table 3).

SHORELINE.—The shoreline zone was dominated by the dwarf herring, Jenkinsia lamprotaenia, which averaged 5.4 fish m⁻² but had a patchy distribution, occurring in 60% of the shoreline samples. This diminutive clupeid, which attains sexual maturity at approximately 45 mm standard length, is a schooling species widely used for bait in the Virgin Islands (Friedlander and Beets, 1997). Wagner (1974) reported that it was one of the most abundant baitfish species in the northern Caribbean. Other dominant taxa include Paraclinus nigripinnis (0.68 m⁻², 80%), Labrisomus bucciferus (0.46 m⁻², 73%), and Gobiesox punctulatus (0.69 m⁻², 47%). Although 18 species were collected exclusively at shoreline stations, only 10 of them are typically restricted to such habitats: Malacotenus versicolor, Stathmonotus gymnodermis, Hypsoblennius exstochilus, Scartella cristata, Gobiesox nigripinnis, G. punctulatus, Tomicodon reitzae, Barbulifer antennatus, Bathygobius soporator, and Ginsburgellus novemlineatus. In contrast, 60 species present in at least three of the other habitat zones were absent from shoreline stations (Fig. 2). Given the wave surge, large number of boulders, relative abundance of algae, and the sparse amount of coral, it is not surprising that the diversity of clingfishes and labrisomid blennies in this zone was relatively high, although few gobies and chaenopsids were collected.

NEARSHORE REEF.—As discussed under methods above, the two stations in this zone were difficult to categorize and the species composition is probably a reflection of the intermediacy of the habitat. *Halichoeres bivittatus, Sargocentron vexillarium, Stathmonotus stahli, Moringua edwardsi*, and *Thalassoma bifasciatum* were dominant at one or both of these stations, but these species were also common in other habitats.

PATCH REEFS IN LAGOON.—In the lagoon zone, *Phaeoptyx conklini* (1.73 m⁻², 87%), *S. stahli* (1.25 m⁻², 100%), *Malacoctenus macropus* (1.16 m⁻², 93%), and *Coryphopterus glaucofraenum* (1.09 m⁻², 93%) dominated, and nine of the ten most common species were present in at least 80% of these 15 stations (Table 3). *Conger triporiceps, Starksia*

Table 3. Ten most common fish species at BIRNM collected with rotenone in each habitat zone at blocknet enclosed stations. Commonness index (mean density

Shorenile (stanons 1–13)					Nearshore Reef (stations 16–17)				
Species	Common index	Mean density	Std Dev	Occur	Species	Common index	Mean density	Std Dev	Occur
Jenkinsia lamprotaenia	3.24	5.40	11.17	09.0	Halichoeres bivittatus	0.83	0.83	0.59	1.00
Paraclinus nigripinnis	0.55	89.0	0.64	0.80	Sargocentron vexillarium	0.58	0.58	0.71	1.00
Labrisomus bucciferus	0.34	0.46	0.55	0.73	Stathmonotus stahli	0.52	1.04	1.47	0.50
Gobiesox punctulatus	0.32	69.0	1.98	0.47	Moringua edwardsi	0.50	0.50	0.24	1.00
Malacoctenus gilli	0.26	0.36	0.56	0.73	Thalassoma bifasciatum	0.46	0.46	0.29	1.00
Acyrtus rubiginosus	0.13	0.25	0.62	0.53	Gnatholepis thompsoni	0.29	0.29	0.18	1.00
Entomacrodus nigricans	0.12	0.20	0.20	09.0	Malacoctenus macropus	0.29	0.29	90.0	1.00
Malacoctenus erdmani	0.12	0.18	0.26	0.67	Stegastes leucostictus	0.25	0.25	0.12	1.00
Stegastes leucostictus	0.08	0.15	0.35	0.53	Malacoctenus gilli	0.25	0.25	0.12	1.00
Ginsburgellus novemlineatus	80.0	0.11	0.24	0.67	Labrisomus guppyi	0.19	0.38	0.53	0.50
Lagoon (stations 18–32)					Backreef (stations 33–38)				
Species	Common	Mean	Std Dev	Occur	Species	Common	Mean	Std Dev	Occur
	index	density				index	density		
Phaeoptyx conklini	1.51	1.73	1.50	0.87	Stathmonotus stahli	4.73	4.73	5.87	1.00
Stathmonotus stahli	1.25	1.25	1.19	1.00	Phaeoptyx conklini	1.69	1.69	1.86	1.00
Malacoctenus macropus	1.08	1.16	1.16	0.93	Malacoctenus macropus	0.81	0.81	0.76	1.00
Coryphopterus glaucofraenum	1.01	1.09	0.92	0.93	Coryphopterus glaucofraenum	0.80	08.0	0.75	1.00
Lythrypnus crocodilus	0.41	0.52	0.50	0.80	Elacatinus pallens	0.61	0.34	0.21	1.00
Gnatholepis thompsoni	0.32	0.34	0.32	0.93	Starksia atlantica	0.34	0.33	0.42	0.83
Coryphopterus dicrus	0.30	0.32	0.31	0.93	Enneanectes altivelis	0.33	0.22	0.21	1.00
Apogon townsendi	0.29	0.43	0.62	0.67	Starksia lepicoelia	0.27	0.27	0.35	0.67
Elacatinus pallens	0.27	0.31	0.31	0.87	Labrisomus guppyi	0.22	0.19	0.12	0.67
Enneanectes altivelis	0.21	0.27	0.30	08.0	Coryphopterus dicrus	0.19	0.28	0.31	0.67

Table 3. Continued.

Forereef (stations 39–45)					Bank/Shelf (stations 46–58)				
Species	Common index	Mean density	Std Dev	Occur	Species	Common index	Mean density	Std Dev	Occur
Phaeoptyx conklini	2.32	2.70	2.75	98.0	Coryphopterus glaucofraenum		1.12	0.92	1.00
Enneanectes altivelis	1.01	1.01	0.87	1.00	Starksia lepicoelia	0.81	0.95	0.88	0.85
Coryphopterus glaucofraenum	0.41	0.48	0.52	98.0	Acathemblemaria aspera	0.65	1.20	2.26	0.54
Starksia lepicoelia	0.41	0.58	0.65	0.71	Phaeoptyx pigmentaria	0.58	0.83	1.23	69.0
Apogon townsendi	0.39	0.54	0.63	0.71	Enneanectes altivelis	0.52	0.56	0.67	0.92
Lythrypnus crocodilus	0.28	0.28	0.27	1.00	Gnatholepis thompsoni	0.48	0.48	0.31	1.00
Phaeoptyx pigmentaria	0.20	0.35	0.44	0.57	Priolepis hipoliti	0.45	0.53	0.76	0.85
Moringua edwardsi	0.18	0.18	0.09	1.00	Apogon townsendi	0.41	0.59	0.73	69.0
Chromis cyanea	0.16	0.37	0.89	0.43	Thalassoma bifasciatum	0.40	0.52	0.48	0.77
Gnatholepis thompsoni	0.14	0.20	0.17	0.71	Haemulon flavolineatum	0.34	1.49	4.13	0.23

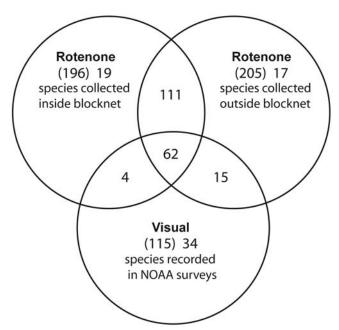


Figure 4. Comparison of number of fish species collected at 58 stations using rotenone inside and outside of blocknet enclosures during July–August, 2001 with 70 NOAA visual surveys (combined transects and point-counts) during August–September, 2001 at BIRNM. Numbers in areas of overlap indicate shared species, numbers in parentheses are total species, and numbers outside parentheses indicate species exclusive for each method.

nanodes, Lythrypnus okapia, Psilotris celsus, and Lactophrys triqueter were apparently rare as they were each encountered on one lagoon patch reef where a single individual was collected.

BACKREEF.—The same four dominant species in the lagoon stations also had the highest commonness index and mean densities in the six backreef samples, and these plus two others (*Enneanectes altivelis* and *Elacatinus pallens*) occurred at every station and were also present at 87%–100% of the lagoon sites. *Stathmonotus stahli* had its highest mean densities (4.73 m⁻²) at the backreef sites. There were no taxa unique to backreef samples. *Cerdale floridana* was shared with only one bank/shelf station but was uncommon at both stations.

Forereef.—Lagoon, backreef, and forereef samples were similar in having high densities of *P. conklini*, *E. altivelis*, and *Coryphopterus glaucofraenum* (Table 3). *Equetus punctatus*, *Hypleurochilus springeri*, and *Pempheris schomburgkii* were encountered only in forereef habitat; the latter species was found in only one small cave.

Bank/Shelf Reefs.—Despite deeper water (> 6 m except station 52), the bank/shelf zone was dominated by *C. glaucofraenum*, *Starksia lepicoelia*, and *Acanthemblemaria apsera*. These species were also common in the lagoon, backreef, and forereef zones. The only records of *Ginglymostoma cirratum*, *Hypoplectrus puella*, *Serranus baldwini*, *Apogon affinis*, *Inermia vittata*, *Holocanthus ciliaris*, *Clepticus parrae*, *Halichoeres pictus*, *Paraclinus grandicornis*, *Starksia melasma*, *Elacatinus chancei*, *Psilotris boehlkei*, *Symphurus arawak*, and *Symphurus ommaspilus* were from bank/shelf stations.

Species Accumulation Curves.—None of the species accumulation curves (Fig. 5) reached asymptotes indicating that more sampling would be required to estimate the total number of fish species in BIRNM reef habitats. Samples from backreef, forereef, lagoon, and bank/shelf habitats had the same general curve as that of all combined rotenone stations. Using incidence-based coverage estimations (Chao and Lee, 1992) on all 58 enclosed rotenone samples, 225 ± 2 (mean \pm SD) species are predicted to be present. Shoreline and nearshore reef stations had a much lower trajectory and likely have substantially fewer species (105 ± 3). Visual surveys by NOAA divers also had a lower curve. Based only on the 70 combined transect and point-count UVC stations made at BIRNM in August–September, 2001, an estimated 146 \pm 2 species were predicted to be present. Clearly, these are underestimates of the total fish diversity at BIRNM despite some curves approaching an asymptote, and highlight the selective bias of the kinds of fishes that can be detected using any single method.

Species Detection Rates.—Each rotenone station took about 1 hr to complete and covered an average of 15.1 ± 2.8 m² (mean \pm standard deviation). Blocknet rotenone stations yielded 196 total species compared to 115 species observed during combined transects and point counts (Fig. 5). An additional 17 species affected by the rotenone were collected only outside the blocknet for a total of 262 species in combined visual and rotenone samples. Sixty-two species were recorded by UVC and also collected with rotenone both inside and outside the blocknet enclosure. Fifty-six percent of the species were detected only by rotenone sampling while 13% were only detected by belt transect or point-count census. By dividing the total number of species by the total area sampled and time each method required, approximations of catch-per-unit area and effort were determined. With rotenone a different species

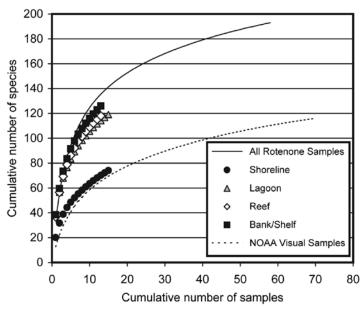


Figure 5. Species accumulation curves by cumulative number of samples for all enclosed rotenone stations (n = 58), shoreline (1–15), lagoon (18–32), reef (33–45), bank/shelf (46–58), and NOAA visual stations (n = 70) at BIRNM during July–September, 2001.

was detected every 17.8 min and $4.5~\rm m^2$ sampled, compared to $12.2~\rm min$ and $168.6~\rm m^2$ for the combined visual consensus.

FISH BIODIVERSITY.—Because St. Croix is centrally located in the tropical eastern Caribbean Sea, as expected, most of the BIRNM fishes are broadly distributed West Indies species. The only annotated list of fishes of St. Croix (Clavijo et al., 1980) included 400 species, and for non-cryptic species agrees reasonably well with those listed in Figure 2. We record the presence of an additional 60 species absent from the earlier list. The majority of these fishes are cryptic species that would be very difficult to detect without the use of rotenone, and include the following families with the number of species additions in parentheses: Gobiesocidae (4); Ophidiidae (4); Bythitidae (5); Gobiidae (13); Labrisomidae (12); Chaenopsidae (5). The following notable records or taxonomic issues are emphasized. The range of *P. boehlkei*, previously known only from the type locality, St. Barthelemy, Lesser Antilles (Greenfield, 1993), is extended to St. Croix; and the diminutive (9.8–18.4 mm standard length) goby Pycnomma roosevelti, which has generally been considered rare was collected at 25 stations. Specimens we identified as C. glaucofraenum all have the pigmentation described by Garzón and Acero (1990) for Coryphopterus tortugae, which we consider to be a junior synonym. We collected two specimens of Emblemariopsis ruetzleri, a recently described chaenopsid (Tyler and Tyler, 1997) previously known only from Belize. The species we refer to as Emblemariopsis sp. appears to represent an undescribed species. Starksia melasma and Starksia smithvanizi are both recently described species (Williams and Mounts, 2003), the former known only from Mona Island off Puerto Rico and our material, and the latter an allopatric sister-species of Starksia fasciata, which is now known to occur only in the Bahamas and Cuba.

Some species were only visually recorded (Table 4) because they are transient pelagics, highly mobile species, or their usual habitat is seagrass beds or open flats (i.e., *Haemulon* spp.) which we did not sample directly. For example, the shrimp-burrow sharing goby *Nes longus* was observed only in an area of soft substrate in the south lagoon.

Discussion

The nondestructive nature of visual surveys allows repeatable observations that can be conducted relatively fast and inexpensively, and accounts for their popularity and wide application in studies of reef fish ecology and management. Point counts and belt transects are reasonably accurate UVC methods for conspicuous fishes, which are generally larger and relatively active or mobile. The behavior of such fishes also makes them more likely to escape from an enclosure net or otherwise avoid the effects of an ichthyocide. The grazing and browsing abilities of some herbivorous fishes (e.g., parrotfishes, surgeonfishes, and damselfishes) affect the distribution, composition, and rates of production of algal assemblages on coral reefs (Choat, 1991; Williams and Polunin, 2001), and UVC is well suited to monitor such fishes. In contrast, morphologically or behaviorally cryptic fishes tend to be relatively small, exhibit a high degree of site fidelity, spend the majority of time hidden from view, or frequent habitats in which they are well camouflaged (Depczynski and Bellwood, 2004). Sale and Douglas (1981), Brock (1982), and Bortone et al. (1986) discuss limitations and errors associated with visual censuses, and some suggestions for improvement have been made (Thresher and Gunn, 1986; Samoilys and Carlos, 2000; Harvey

Table 4. Fish species observed at BIRNM in July–September of 2001, but not taken at 58 rotenone stations; species with * were observed only by NOAA divers conducting underwater visual censuses.

Family	Species	Common name
Dasyatidae	Dasyatis americana	Southern stingray
Mylobatidae	*Aetobatus narinari	Spotted eagle ray
Congridae	*Heteroconger longissimus	Brown garden eel
Syngnathidae	*Hippocampus reidi	Longsnout seahorse
Dactylopteridae	*Dactylopterus volitans	Flying gurnard
Serranidae	*Epinephelus adscensionis	Rock hind
Serranidae	*Hypoplectrus unicolor	Butter hamlet
Serranidae	Mycteroperca tigris	Tiger grouper
Serranidae	*Serranus tortugarum	Chalk bass
Malacanthidae	*Malacanthus plumieri	Sand tilefish
Echeneidae	*Echeneis naucrates	Sharksucker
Carangidae	*Caranx crysos	Blue runner
Carangidae	Caranx ruber	Bar jack
Lutjanidae	*Lutjanus analis	Mutton snapper
Lutjanidae	Lutjanus apodus	Schoolmaster
Lutjanidae	*Lutjanus griseus	Gray snapper
Lutjanidae	*Lutjanus synagris	Lane snapper
Gerreidae	Gerres cinereus	Yellowfin mojarra
Haemulidae	*Haemulon aurolineatum	Tomtate
Haemulidae	*Haemulon carbonarium	Caesar grunt
Haemulidae	*Haemulon chrysargyreum	Smallmouth grunt
Haemulidae	*Haemulon sciurus	Bluestriped grunt
Mullidae	*Mulloidichthys martinicus	Yellow goatfish
Pomacanthidae	*Holacanthus tricolor	Rock beauty
Pomacanthidae	*Pomacanthus arcuatus	Gray angelfish
Kyphosidae	*Kyphosus sectatrix	Bermuda chub
Scaridae	Scarus guacamaia	Rainbow parrotfish
Chaenopsidae	*Chaenopsis ocellata	Bluethroat pikeblenny
Gobiidae	Nes longus	Orangespotted goby
Ptereleotridae	*Ptereleotris helenae	Hovering goby
Sphyraenidae	*Sphyraena picudilla	Southern sennet
Scombridae	*Scomberomorus regalis	Cero
Paralichthyidae	*Syacium sp. (? papillosum)	Dusky flounder
Balistidae	*Balistes vetula	Queen triggerfish
Ostraciidae	*Acanthostracion polygonius	Honeycomb cowfish
Diodontidae	Diodon holocanthus	Balloonfish

et al., 2004). Despite awareness of these biases, the ecological significance of small cryptic fishes has been largely ignored and exclusive reliance on UVC methods and fisheries data for estimates of biodiversity, community structure, and abundances is widely practiced. Several recent authors (Ackerman and Bellwood, 2000; Willis, 2001; Collette et al., 2003) discuss the need for accurate assessments of cryptic fish assemblages and why UVC is inadequate. Ackerman and Bellwood (2002) concluded "if the goal of the sampling is to quantitatively record all small fish in an area, then rotenone and the use of an enclosed site remains the most applicable method."

Knowlton (2001) noted that as we computerize and analyze existing databases to assess reef biodiversity, we should remember that most reef organisms are not only numerous but usually uncounted; and this certainly applies to cryptic fishes. Are accurate estimates of fish biodiversity important? Recent studies of larval fish behavior (Leis and McCormick, 2002), oceanographic processes (Cowen, 2002), and genetic structure of reef fishes (Rocha, 2004; Rocha et al., 2005) indicate that knowledge of pelagic larval duration and current patterns are not reliable predictors of faunal connectivity. Traditional assumptions about larval fish dispersal potential are challenged by research indicating that reef fish connectivity is more complex than previously thought (Leis, 2002; Lester and Ruttenberg, 2005). Thus, reliable inventories of species throughout their ranges are essential to define distributional limits, investigate geographic variation, and determine which species are actually present. One problem with visual census data is the tendency to accept identifications without adequate or independent confirmation.

Voucher specimens and archived collection data are extremely important to independently verify historical and contemporary identifications, which for cryptic fishes and juveniles of others often require the use of a microscope and recent taxonomic literature. This validated biodiversity is essential to ecological analyses of geographic and temporal trends (Cotterill, 1995). In order to understand the energy flow and population dynamics of the reef ecosystem, knowledge of the organisms and their community structure, relative abundances, and connectivity is necessary.

Biodiversity hotspots are of particular interest to resource managers, however, unlike terrestrial systems where the majority of species have small ranges, in reef ecosystems high diversity areas arise primarily from the combined contributions of relatively widely distributed fishes (Hughes et al., 2002). Caribbean families with the greatest number of species are predominately cryptic reef fishes (e.g., Gobiidae, Chaenopsidae, and Labrisomidae), many with restricted distributions.

Our data show that a significant proportion of the BIRNM reef fish assemblage has been underrepresented or missed in visual censuses. Only 36% of the 228 species sampled with rotenone were visually detected, 70% of the 115 species visually detected were also collected with rotenone, and 31% of the 262 total species were common to both techniques. In a comparison of rotenone samples versus UVC conducted on the Great Barrier Reef over a 5-yr period, Ackerman and Bellwood (2000) found that of 205 total species recorded, only 33.6% were common to both techniques, with 50% of the individuals and 40% of the species overlooked by visual methods. It should be noted that our study was not designed to test for differences in accuracy of techniques and the UVC data we used for the comparisons are only broadly equivalent in time and space. However, our results are consistent with other studies (Ackerman and Bellwood, 2000; Collette et al., 2003; Dennis et al., 2005) that document the need for multiple types of censuses if comprehensive biodiversity assessment is a goal of the research.

Because adults of most cryptic reef fishes are sedentary, obligatory reef species frequently occurring in high densities with populations less directly impacted by fisheries, they may be better indicators of localized pollution or other adverse environmental conditions than fishes commonly recorded using UVC. Although the biomass contribution of cryptic fishes to the total standing stock may seem insignificant due to their generally small sizes, their contribution to reef ecology may be disproportionately important, with up to 25% of the energy flow of reef fishes

attributable to cryptobenthic species (Ackerman and Bellwood, 2002). By virtue of their small sizes and abundances, cryptic fishes are potentially available to a wider range of predators. Cryptic fishes provide important trophic links between detritus and primary producers, invertebrate consumers, and many piscivorous reef fishes (Depczynski and Bellwood, 2003; Ackerman et. al., 2004). Static biomass estimates do not adequately reflect the rapid turnover and high productivity of small fishes which typically have shorter life cycles (Allen et al., 1992; Depczynski and Bellwood, 2005). Biogeography can play a pivotal role in providing the scientific basis for marine conservation planning (Lourie and Vincent, 2004) but distributional data should be based on what is actually present rather than just what can be seen. By combining the strengths of UVC with those of rotenone samples, we can make more meaningful comparisons with other reef sites and obtain a more complete assessment of the entire ichthyofauna.

MISCONCEPTIONS ABOUT ROTENONE.—There is a widely held misconception that rotenone is detrimental to corals, and this has contributed to strong opposition to its use. Commercial emulsified rotenone solutions contain petroleum derivatives and other solvents that are the harmful agents (instead of the rotenone) to corals and other marine invertebrates. Jaap and Wheaton (1975) reported that undiluted rotenone, in the form of a commercial preparation, Chem Fish Collector, which is no longer manufactured, had no deleterious effect on five species of octocorals, but caused permanent damage to four of six species of scleractinians that were tested. Damage occurred when undiluted rotenone was applied directly to the test organism, a procedure that was not in accord with label directions or general practice. Gilmore et al. (1981) conducted laboratory bioassay experiments and field comparisons of various rotenone compounds and solutions and made the following important observation: "Our data indicate that the adverse reactions seen with the application of emulsified rotenone solutions on living corals observed by other workers ... may be limited to emulsified rotenone solutions." Collette et al. (2003) reported, and our experience confirms, that powdered rotenone targets fishes selectively and does not kill invertebrates (except possibly cephalopods). Rotenone powder requires an emulsifier and, while there may be other environmentally safe surfactants, biodegradable liquid detergents seem to be very acceptable for that purpose.

Rotenone is considered a poison, a term with very negative connotations. However, the diluted concentrations of rotenone used for collecting are such that any fishes killed can be safely consumed by birds (Finlayson et al., 2000) and humans (although the U.S. Food and Drug Administration has not approved this practice). In aquatic environments, rotenone becomes ineffective following dilution, detoxifies naturally from biological action, breaks down rapidly in warm water (20°C) and "poses no lasting threat to the environment" (Sousa et al., 1987).

Relative Impact of Rotenone on Fish Assemblages.—Because rotenone is such an effective and nonselective ichthyocide, there is often reluctance to allow its use. The amount of area affected at a rotenone station can be planned and often is a miniscule proportion of the total habitat, and a correspondingly small sample of the fish community. Although more studies are needed, available data indicate that recovery of defaunated sites following the application of rotenone begins almost immediately (Smith, 1973; Smith and Tyler, 1975; Rosa et al., 1997). It is important to remember that any "snapshot" of fish assemblages should be interpreted carefully considering the dynamic nature of the coral reef community (Sale, 1991), and pro-

cesses affecting site-attached species on small isolated patch reefs may not necessarily be applicable to those inhabiting large, well-connected reef mosaics (Ault and Johnson, 1998). With the exception of eels, large individuals of most species tend to be wary and are seldom collected with rotenone because they immediately leave the area at the first approach of divers. This is also true of most highly mobile or transient species (e.g., bar jacks, *Caranx ruber*, are very common at BIRNM but were not taken at any rotenone station).

CLOVE OIL AS AN ALTERNATIVE TO ROTENONE.—Clove oil has been suggested as an alternative to rotenone for general inventory of cryptic fishes (Ackerman and Bellwood, 2002) primarily because fish affected outside the sample site can recover from the anaesthetic and "swim away" (Munday and Wilson, 1997). Unfortunately, clove oil has its own limitations. Properties of clove oil make it impractical to sample more than a few square meters of habitat, a smaller number and variety of the fishes actually present are likely to be captured, greater effort will be required, and some amount of consumptive sampling will still occur. To be effective, clove oil mixtures must be applied at much higher concentrations than rotenone, and thus a larger volume of clove oil must be used to sample the same amount of habitat. Dispersal is also more problematic. This can be partially alleviated by covering small sites with an impermeable nylon cloak (Ackerman and Bellwood, 2002) but requires the assistance of a team of divers. Clove oil is positively buoyant, difficult to dispense, and is typically mixed with ethanol, a combination which causes some corals to bleach (Erdmann, 2000). Susceptibility of fishes to clove oil is interspecifically variable (Griffiths, 2000), and concentrations that are satisfactory for some species will be ineffective or lethal to others. Rotenone inhibits cellular respiration of fishes and the usual reaction is emergence from their hiding places (including those buried in the substratum; e.g., snake eels and sand stargazers). In contrast, clove oil-anaesthetized fishes are much less likely to swim out into the open where they can be collected. Fish collectors for the marine aquarist market typically visually locate and apply anaesthetics to individual target fishes that they then closely monitor, often reapplying the anaesthetic, until the fish is finally captured. As with rotenone, cryptic reef fishes collected with anaesthetics must be brought to the surface and handled in order to be sorted, identified, counted, and measured. If the purpose of anaesthetics is to avoid consumptive sampling, then captured fish must be maintained in well-oxygenated containers. Despite careful handling, some amount of stress will occur. Even if they initially survive the experience, anaesthetized fishes may ultimately succumb to the physiological stress or be more vulnerable to predation or disease.

Summary.—While visual census techniques are popular nonconsumptive methods widely used to monitor coral reef fishes, nearly half of the ichthyofauna is either undetected or undercounted. Complete baseline inventories and monitoring data are essential for understanding long-term trends in MPAs. A combination of visual and rotenone methods gives a more complete and accurate assessment of reef fish biodiversity and the methods are complementary. Repeatable and nonconsumptive visual methods can better address the dynamic trends in the fish community structure while only rotenone sampling can reveal the myriad of cryptic fishes that are also important yet understudied. Rotenone studies are labor intensive, require greater taxonomic expertise, and are more expensive when specimen curation is included in the costs.

The following key steps will help ensure that rotenone continues to be allowed for research purposes and knowledge of cryptic reef fishes increases accordingly: (1) Rotenone should not be used without first notifying local authorities and obtaining all required permits. The use of rotenone to collect fishes should only be allowed for clearly defined research purposes; (2) Select sample sites carefully to avoid popular public areas; (3) Apply the minimum amount of rotenone required to sample an area that can be reasonably and completely searched by available divers and never in warm shallow bays or other confined areas when the tide or current is, or soon will be, incoming; (4) Where practical, enclose sites with blocknets so reasonably accurate measurements of abundance per unit of habitat can be obtained;. (5) Properly preserve and deposit specimens in an institution with an established reputation of ichthyological research and history of collection support, preferably one with an on-line searchable database. Long-term support and maintenance of fish collections continues to be a critical issue (Poss and Collette, 1995), but these materials allow independent confirmation of identifications by both contemporary and future workers and serve as an important archive of the past; and (6) Resource managers should have access to all records associated with and publications resulting from the specimen database.

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